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Constructing a hybrid species distribution model from standard large-scale distribution data

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ABSTRACT

Species range shifts under climate change have predominantly been projected by models correlating species observations with climatic conditions. However, geographic range shifting may depend on biotic factors such as demography, dispersal and species interactions. Recently suggested hybrid models include these factors. However, parameterization of hybrid models suffers from lack of detailed ecological data across many taxa. Further, it is methodologically unclear how to upscale ecological information from scales relevant to ecological processes to the coarser resolution of species distribution data (often 100 km^2 or even 2500 km^2). We tackle these problems by developing a novel modelling and calibration framework, which allows hybrid model calibration from (static) presence-absence data that is available for many species. The framework improves understanding of the influence of biotic processes on range projections and reveals critical sources of uncertainty that limit projection reliability. We demonstrate its performance for the case of the butterfly Titania's Fritillary (*Boloria titania*).

1. Introduction

Projections of species distributions under changing environmental conditions are needed to support the conservation of biodiversity (Dawson et al., 2011; Pereira et al., 2010). Most models (such as bioclimatic envelope models, synonyms: ecological niche models, habitat models or species distribution models) statistically correlate species observations and environmental conditions (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000; Yalcin and Leroux, 2017). Because of their correlative calibration approach, we refer to them as correlative species distribution models (C-SDMs). The correlative approach takes advantage of the type of widely available data, such as raster maps of species occurrence and environmental factors, usually derived from atlas data. The models, however, often for technical reasons (Singer et al., 2016), ignore key biotic mechanisms that affect species distributions (Urban et al., 2016).

Recent methodological advances suggest ways to enhance structural realism of species distribution models by incorporating biotic factors (Bocedi et al., 2014; Cabral et al., 2017; Evans et al., 2016; Kissling et al., 2012; Schurr et al., 2012; Talluto et al., 2016; Zurell, 2017) and have been shown to improve range projections (Zurell et al., 2016). One approach are hybrid species distribution models (H-SDMs; Dormann et al., 2012; also called niche population models Fordham et al., 2013). H-SDMs are based on C-SDMs that constitute filtering by the abiotic environment but add further relevant biotic processes or factors, such as interspecific interactions (Kissling et al., 2010; Meier et al., 2012; Schweiger et al., 2012), individual variability and local adaptation (Swab et al., 2015), dispersal or transport (Buse and Griebeler, 2011; Chapman et al., 2016; De Cáceres and Brotons et al., 2012; Kramer-Schadt et al., 2004), or demography (Keith et al., 2008). These studies used additional ecological knowledge to parameterize the biotic processes, and showed differences in range projections compared to such based on abiotic environmental information only.

However, for many species, ecological process knowledge is lacking. Therefore, it would be desirable to parameterize H-SDMs from widely available data similarly to C-SDMs. Clearly such an endeavor has its limitations, because model projections cannot be more reliable than the information from which they are constructed. Missing knowledge on model and process structure or model parameters can compromise projection reliability (Singer et al., 2016). Nevertheless, we will show

Abbreviations: C-SDM, correlative species distribution model; G-ECM, grid cell extinction-colonization model; H-SDM, hybrid species distribution model

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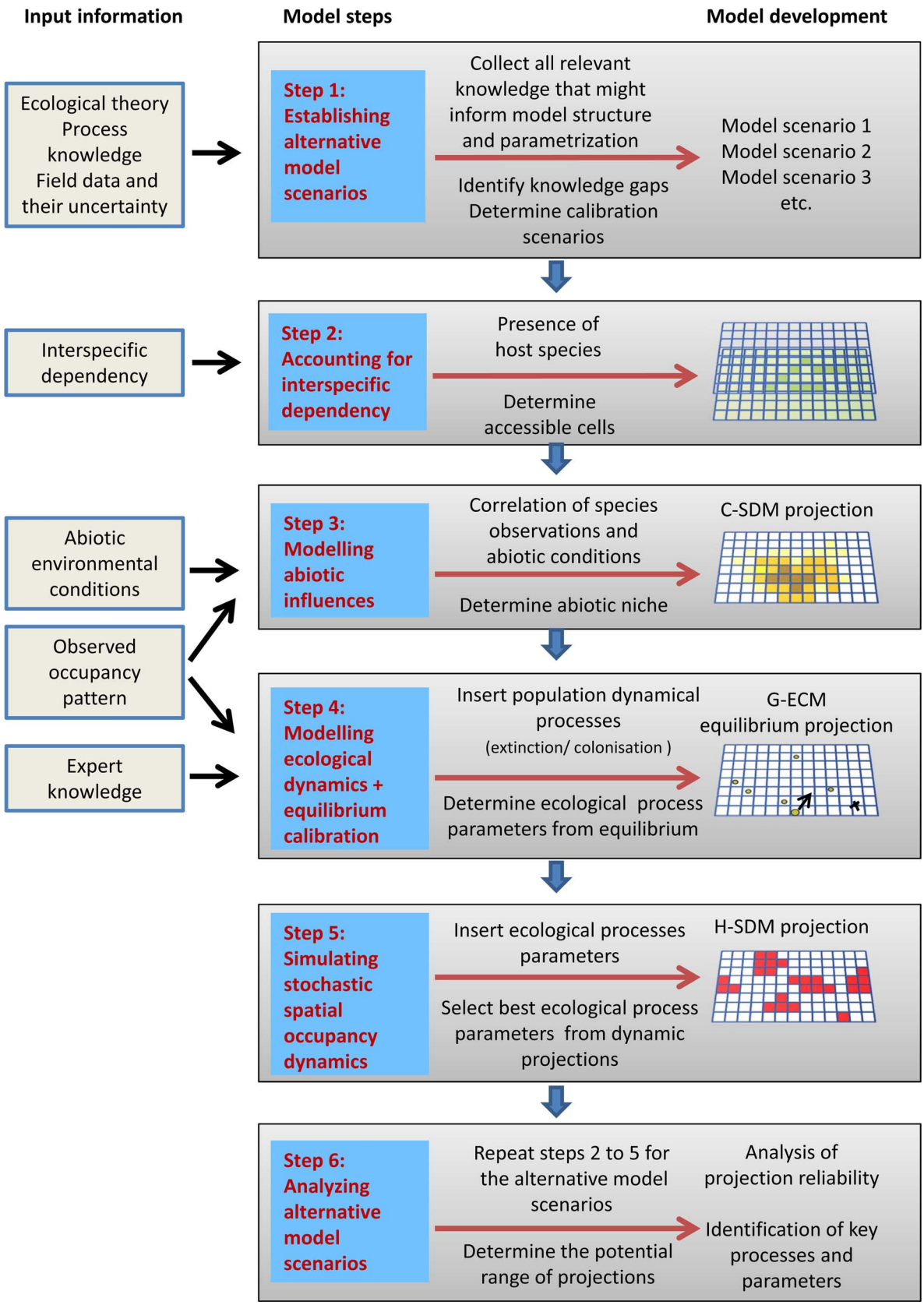

Fig. 1. H-SDM modelling framework. Embedded in a framework of model critique, the H-SDM hierarchically combines two submodels, a correlative species distribution model (C-SDM) and a grid-cell extinction colonization model (G-ECM). In a knowledge survey, available and lacking information is identified and condensed in model scenarios (step 1). Interspecific dependency on host species limits spatial extent (step2). From environmental filtering, the C-SDM projects abiotic grid cell suitability for each geographic grid cell (step 3). This grid cell suitability affects population dynamical processes in the G-ECM. Parametrization via the G-ECM equilibrium solution (step 4) is further improved by stochastic H-SDM projections (step 5). Steps 2–5 are repeated in uncertainty and sensitivity analyses (step 6). Models (right column) and data (left column) are linked by modelling steps (central column). For further information refer to Sec. 2.2.

that, hybrid models can improve species range projections based on generally available biogeographic information such as presence-absence data.

In this study, we develop a hybrid modelling framework consisting of six steps that allows including and calibrating demographic processes and dispersal from currently available maps on species occupancy and environmental variables. To demonstrate its merits the framework was exemplarily applied to project the range of the holarctic butterfly Titania's Fritillary (*Boloria titania*), almost monophagously feeding as larvae on Adderwort (*Bistorta officinalis*). We analyzed the calibration framework with respect to its ability to shrink parameter and structural uncertainty, and studied the consequences of remaining uncertainty for projection reliability.

2. Material and methods

We developed a generic framework (Fig. 1) to construct H-SDMs from currently available data (left boxes in Fig. 1). The type of data that is generally available for species distribution modelling comprises variables on abiotic environmental conditions (third left box in Fig. 1) and maps of observed species occupancy patterns (fourth left box in Fig. 1). However, information on biotic processes is often limited to general theory (first left box in Fig. 1), information on interspecific dependencies (second left box in Fig. 1), or expert knowledge (fifth left box in Fig. 1).

In Sec. 2.1 we describe major challenges arising from data limitations, and suggest solutions. In Sec. 2.2, we operationalize these solutions in a protocol for the H-SDM model construction and calibration.

2.1. Major challenges and suggested solutions

Challenge 1: Lack of information

We identify two types of knowledge gaps that can limit projection reliability of species distributions: structural gaps and data gaps.

Structural gaps, e.g. concerning the relevant environmental drivers or the formulation of ecological response processes to these drivers, compromise the structure of the model resulting in structural uncertainty. Data gaps or uncertainty of data measurements compromise model parameterization resulting in parameter uncertainty. Both structural and parameter uncertainty reduce projection reliability (Singer et al., 2016).

Solution 1: Knowledge gap analysis

Identifying knowledge gaps prior to implementing the model helps addressing them adequately by (1) filling the gaps with complementary information (e.g. from targeted empirical studies; Bierman et al., 2010; Manceur and Kühn, 2014), by (2) assessing their impact on projection reliability or by (3) projecting metrics that are robust in spite of missing knowledge (Gould et al., 2014). Focusing here on models with a defined endpoint, i.e. projection of spatiotemporal species occurrence, we are mainly concerned with the second aspect.

Consequences of structural gaps can be assessed by implementing alternative model formulations (as suggested in pattern oriented modelling; Grimm and Railsback, 2011). To shrink the number of alternative models, model formulations can be weighted or even rejected, based on their plausibility. Plausibility criteria might comprise statistical parsimony, ecological theory, expert knowledge (Gallien et al., 2010) or post hoc sensitivity analyses (Saltelli et al., 2000). Consequences of data gaps can be assessed by parameter uncertainty analyses (Saltelli et al., 2000). Finally, the joint impact of structural and data gaps on projection reliability can be estimated in ensemble projections of the alternative models and parameterizations.

Challenge 2: Coarse spatial resolution impedes detailed description of ecological processes

The coarse spatial resolution of available species distribution data exceeds the fine spatial resolution of ecological processes (Soberon and Nakamura, 2009). Therefore, distribution data contains only up-scaled information about spatial ecological processes and biotic responses to the environment.

Solution 2a: Grid cell – extinction colonization model (G-ECM) aggregates local population dynamics and dispersal

We follow suggestions of applying a metapopulation approach to implement ecological dynamics in species distribution models (Talluto et al., 2017; Thuiller et al., 2013). For metapopulations at landscape scale, local dynamics within patches are aggregated and patch-occupancy patterns reflect small-scale ecological processes (Etienne et al., 2004; Grimm et al., 2004; Hanski, 1994). This metapopulation approach has been transferred to larger spatial scales of geographic grid cells (e.g. Buse and Griebeler, 2011; De Cáceres and Brotons et al., 2012). We implement the approach as a grid cell – extinction colonization model (G-ECM; see Section 2.2.4) that tracks species occupancy dynamics at geographic grid cells. However, we point out that, in contrast to metapopulations (Hanski, 1992; ter Braak et al., 1998), scaling rules of ecological processes are unclear at the biogeographic scale (Barwell et al., 2014; Henle et al., 2014; Pearson et al., 2004). Therefore, a strict ecological interpretation of the extinction and colonization parameters is not possible at the large geographic grid scale.

Solution 2b: Interspecific dependency as a geographic filter for species distributions

Small-scale interspecific interactions can affect species distributions at large scales, and prior knowledge on interspecific interactions can refine projections of species distributions (Kissling et al., 2012; Singer et al., 2016; Wisz et al., 2013). Particularly, if one species depends on other host species to complete its lifecycle, the distribution of the dependent species is constrained by presence of the host species. Consequently, we suggest limiting the distribution of a species by the distribution of its host species, i.e. applying the spatial distribution of host species as a geographic filter (Schweiger et al., 2012, 2008). This filtering approach is suitable for predominantly unidirectional interactions (called here interspecific dependency; e.g., commensalism, mutualism or parasitism with weak feedbacks). A recently suggested advancement (Staniczenko et al., 2017) based on Bayesian networks promises to account for more complex interspecific interactions (e.g., competition, facilitation or predator-prey interactions). However, caution should be taken concerning interspecific interactions with strong feedbacks because feedbacks can lead to complex effects on range-dynamics (Singer et al., 2016, 2013).

Challenge 3: Lack of temporal information

Temporal information is essential to calibrate dynamics of species distributions (De Cáceres and Brotons et al., 2012). In extinction-colonization models, parameters should be estimated from turnover data or a set of occupancy maps taken at different points in time (Etienne et al., 2004; Moilanen, 2004, 1999; O'Hara et al., 2002; ter Braak and Etienne, 2003). Recent methods to calibrate dynamic species distribution models apply hierarchical likelihood-based techniques (Cabral and Schurr, 2010; Evans et al., 2016; Marion et al., 2012; Pagel and Schurr, 2012; Talluto et al., 2017). These methods require detail in spatiotemporal occupancy (Talluto et al., 2017) or abundance time series (Pagel and Schurr, 2012). However, in atlas data, temporally resolved information is usually pooled to gain spatial coverage. The current lack of time series data across large extents impedes grid cell turnover estimates for most species (but see Schurr et al., 2012 for suggestions to improve the situation).

Solution 3a: Sequential H-SDM calibration

We use an H-SDM (consisting of a C-SDM coupled with a G-ECM) and parameterize C-SDM and G-ECM in subsequent steps, which is a common approach (Dormann et al., 2012). However, sequential parameter estimation can introduce bias in model calibration. Particularly, in the initial calibration step, the C-SDM might confound patterns from biological processes for effects from abiotic filters (Schurr et al., 2012). As a consequence, the G-ECM calibration in the second step might not be based on the full biotic information, or both calibration steps might pick up the biotic information, resulting in double-accounting for the

biotic impact (Gallien et al., 2010). Nevertheless, this assumption is widely used in H-SDM approaches (e.g. Holloway et al., 2016; Keith et al., 2008; Meier et al., 2012; Regan et al., 2012). To assess and cope with potential bias in parameter estimates, detailed analysis of the dynamic model projections have to be performed.

Solution 3b: Equilibrium calibration followed by simulations of the stochastic spatiotemporal dynamics

We resort to calibrating the G-ECM assuming the species is in equilibrium and its equilibrium distribution is represented by its distribution map. The equilibrium assumption has been successfully applied to calibrate dynamic metapopulation models from single patch occupancy patterns (pioneered by Hanski, 1994) and to calibrate a demographic plant species distribution model from a single abundance pattern (Cabral and Schurr, 2010). Yet, we point out that calibration of a dynamic model from a single snapshot can cause biased parameter estimates (Moilanen, 2000). This may happen if the species distribution is not in equilibrium, such as for invasive or currently range changing species. Therefore, after equilibrium calibration we proceed with simulations of the explicit stochastic occupancy dynamics of the H-SDM.

2.2. Protocol of the generic modelling and calibration framework

These challenges and our solutions are the basis for the six steps of our generic hybrid modelling framework (Fig. 1, right): (1) identifying knowledge gaps and accounting for them in a set of plausible alternative model scenarios, (2) accounting for interspecific dependency, (3) estimating the abiotic species niche through environmental filtering in a C-SDM, (4) modelling the ecological dynamics based on a G-ECM (taking into account both interspecific dependency - step 2 and abiotic conditions - step 3) and calibrating the parameters assuming the system is in equilibrium, (5) simulating the stochastic spatiotemporal dynamics of occupancy of the H-SDM for different calibrated parameter combinations to further confine parameter ranges, and (6) repeating the previous steps for the alternative model scenarios identified in step 1. With each step, we aim at extracting additional information on the species' environmental response from the species spatial occupancy pattern. These steps are now explained in detail and can be followed in Fig. 1.

2.2.1. Step 1: establishing alternative calibration scenarios

From an analysis of knowledge gaps, we suggest constructing "model scenarios" that describe alternative model formulations in accordance with the available knowledge about the system. For example, if lack of knowledge on a species dispersal pattern impedes resolving the dispersal mechanism, different likely dispersal kernels should be considered in alternative model scenarios. If several knowledge gaps exist, the study design should account for interactions among sources of uncertainties (e.g. in a full-factorial design).

2.2.2. Step 2: accounting for interspecific dependency

Known interspecific dependencies of the species are taken into account to limit its spatial extent. In all modelling steps only grid cells are accessible on which host species are present.

2.2.3. Step 3: modelling abiotic influence

C-SDMs are used to estimate the suitability of grid cells. A large variety of modelling algorithms exists ranging from more traditional regression-based methods, such as Generalized Linear Models or Generalized Additive Models, to more advanced machine-learning methods, like Boosted Regression Trees or MAXENT, with different advantages and shortcomings (e.g. Elith et al., 2006). The choice of the algorithm usually depends on the requirements like interpolation ability or model transferability (e.g. Heikkinen et al., 2012) and the reliability of absence data, e.g. presence-only, presence-background or presence-absence methods. Within our framework we need reliable absence data (see below) and thus respective methods should be used. In all modeling approaches we suggest to consider interactions among environmental variables as well as non-linear responses of species to environmental variables. We strongly recommend to avoid overfitting by proper variable selection or regularization procedures. The output of presence-absence methods usually are occurrence probabilities which depend on the prevalence of the species. For the subsequent G-ECM calibration (step 4), resulting occurrence probabilities should be centered at a prevalence of 0.5. Therefore, we suggest weighting absences to ensure a prevalence of 0.5 (Maggini et al., 2006).We interpret the projected probability of species occurrence as the suitability of abiotic environmental conditions for the species, which we call grid cell suitability $H_i(t)$ of grid cell i at time t. $H_i(t)$ covers the spatial environmental heterogeneity among grid cells and has the potential to consider environmental change over time.

With grid cell suitability $H_i(t)$ we link abiotic information with ecological processes (step 4), following previous approaches (Buse and Griebeler, 2011; De Cáceres and Brotons et al., 2012; Meier et al., 2010; Swab et al., 2015):

2.2.4. Step 4: modelling ecological dynamics and equilibrium calibration

To track ecological dynamics, we implement a grid cell-extinction colonization model (G-ECM) at the spatial scale of geographic grid cells. In the G-ECM, the occupancy of a grid cell can change from two stochastic population dynamical processes. These are species extinction from a previously occupied cell or colonization of a previously empty cell. Both population dynamical processes are applied in each modelled time step and act simultaneously. They are defined as follows:

Extinction: A species in grid cell i goes extinct at time t with extinction probability

$$E_i(t) = \min(1, e \bullet (1 - H_i(t))) \tag{1}$$

where $H_i(t)$ denotes the cell suitability estimated in the C-SDM (step 3) for all accessible cells (step 2). Eq. (1) assumes a linear decline of $E_i(t)$ with increasing grid cell suitability $H_i(t)$. Model parameter e describes the ability of the species to cope with local habitat conditions and scales with time step length and grid cell size.

Colonization: An empty accessible (step 2) cell i is colonized by a species in time step t with probability

$$C_i(t) = 1 - (1 - c)^{I_i(t)} \tag{2}$$

where c is a parameter that indicates an individual´s ability to establish. $I_i(t)$ denotes the number of immigrants arriving at the empty cell i. We assume that immigrants can originate only from grid cells that are occupied in the previous time step t-1. Therefore,

$$I_i(t) = M \bullet \sum_{j \neq i} g(d_{ij}) \bullet J_j(t-1) \tag{3}$$

where M is the number of emigrants per grid cell, $J_j(t-1)$ is occupancy of cell j at time step $t-1$. $g(d_{ij})$ denotes a dispersal kernel (depending on distance d_{ij} between grid cells i and j). Explicit modelling of dispersal is rare in species distribution modelling (Holloway and Miller, 2017), although the inclusion of probabilistic dispersal kernels $g(d_{ij})$ can improve projections of species distributions (Holloway et al., 2016).

Equilibrium calibration: We follow the incidence function approach (Hanski, 1994) that is technically suitable to calibrate the model parameters from the equilibrium state of grid cell occupancy $\overline{J_i}$ (Etienne et al., 2004):

$$\overline{J_i} = C_i / (C_i + E_i) \tag{4}$$

where we assume constancy of grid cell occupancy J_i during time steps t and $t-1$, which is a reasonable approximation for the quasi-stationary equilibrium state (Hanski, 1999). Inserting Eqs. (1)–(3) into (4) we derive

$$\overline{J_i} = \frac{1 - (1 - c)^{M \bullet \sum_{j \neq i} g(d_{ij}) \bullet J_j}}{1 - (1 - c)^{M \bullet \sum_{j \neq i} g(d_{ij}) \bullet J_j} + \min(1, e \bullet (1 - H_i(t)))} \tag{5}$$

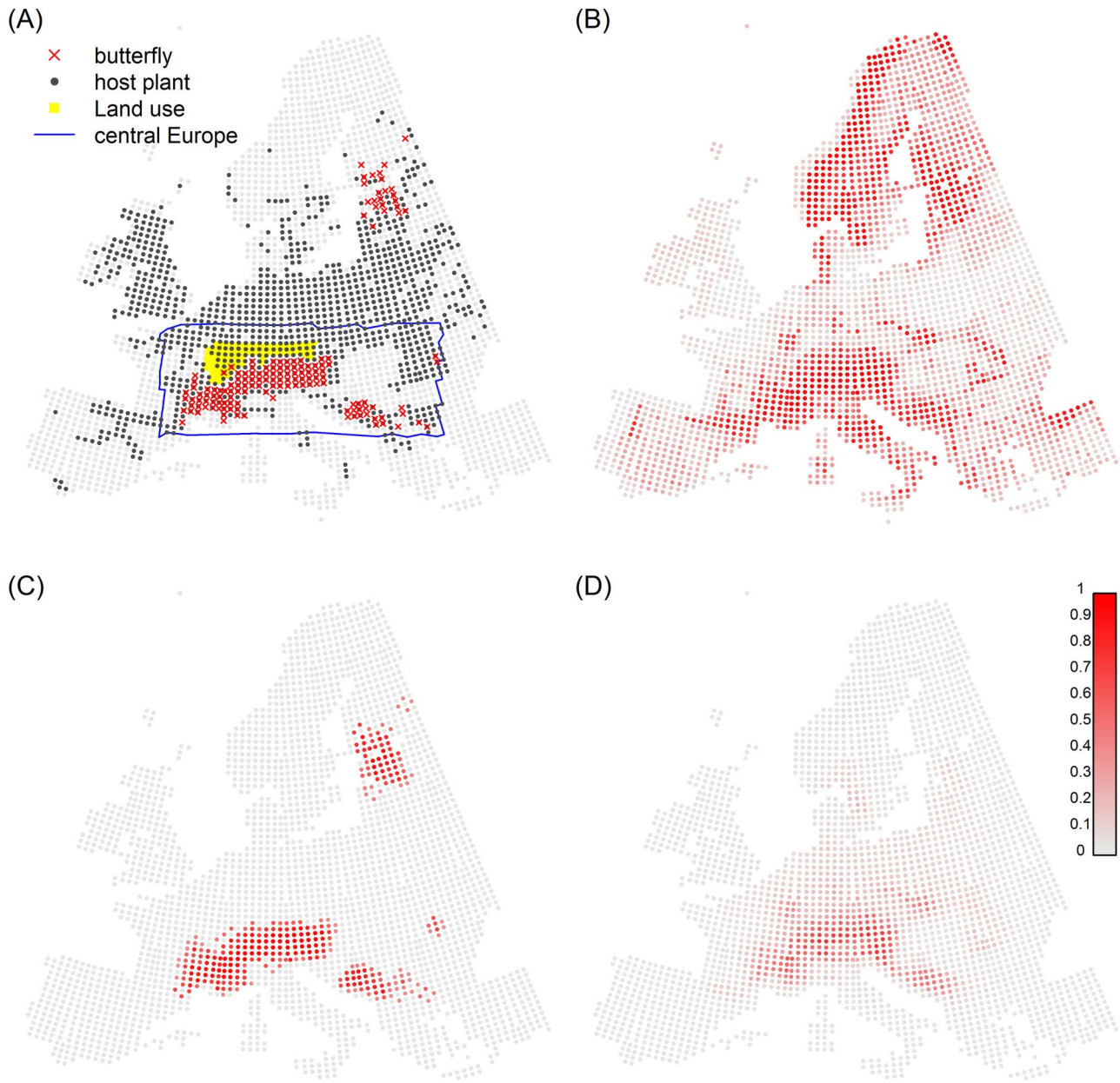

Fig. 2. (A) Presence-absence data and model scenarios as well as (B) mean projected probability of butterfly (Boloria titania) occurrence H_i from C-SDM (note that grid cell suitability resulting from the C-SDM does not consider host plant dependency and thus includes grid cells where its host plant Bistorta officinalis is lacking), (C) occurrence $\overline{J}_i$ from all 80 selected suitable parameter sets of the equilibrium calibration procedure, (D) occurrence $\overline{J}_i$ from all 160 selected H-SDM projections which corresponds to 16,000 repetitions. In (A): host plant presence (dark gray dots), butterfly presence (red crosses), artificially inflated butterfly occupancy to test land use constraints on butterfly occupancy in model scenario OL (yellow area), confined extend in model scenario EC (surrounded by blue line). In (B - D): red scale indicates the projected probability of butterfly occurrence (dark means higher probability – see color scale). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Eq. (5) links grid cell suitability as well as demographic and dispersal parameters to equilibrium grid cell occupancy $\overline{J}_i$. Parameter values can be estimated from Eq. (5) by minimizing the negative log likelihood

$$\overline{L}(P, O) = -\sum_{i=\text{all occupied cells in } O} \ln(\overline{J}_i(P)) + \sum_{i=\text{all empty cells in } O} \ln(1-\overline{J}_i(P)) \tag{6}$$

for the observed occupancy O and parameter set P.

As mentioned above, our modelling framework assumes reliable presence-absence data. False absences could affect G-ECM calibration in several ways (see Moilanen, 2002 in the context of metapopulation model calibration). False absences of high quality grid cells might increase estimates of grid cell extinction rate. Additionally, distances among occupied cells would appear larger due to missing occupied cells, which might result in over-estimation of dispersal distances and colonization success.

The calibration can be supported by potentially available ecological information (e.g. expert or anecdotal knowledge on species dispersal or local extinction risk, Fig. 1 bottom left). This often coarse information can indicate reasonable parameter ranges and filter out unrealistic parameter estimates.

Selection of parameter sets: We suggest a hierarchical latin hypercube design to estimate likely parameter values from Eq. (6) applying rejection sampling. Latin hypercube rejection sampling (LHS) is commonly applied for the calibration of complex ecological models (Hartig et al., 2011; Jakoby et al., 2014). The structure of Eq. (5) allows splitting the parameter space in two lower dimensional parameter

spaces: one for the colonization and extinction related parameters c and e, the other containing dispersal kernel parameters. This splitting reduces computation time, because estimation of complex dispersal kernels for long distances can be computationally costly. However, the splitting destroys homogeneity of the LHS. To avoid under-sampled areas of the parameter space, the sample size in each of the split samples has to be high.

In tests we found that G-ECM calibration can suffer from equifinality (i.e. different parameter combinations might equally likely fit the data). Equifinality leads to uncertainty about the best suitable parameterization. To account for this uncertainty, we suggest selecting several 'best' parameter sets that result in low negative log likelihood values (Eq. (6)). The amount of best parameter sets should be adjusted according to flatness of the likelihood function and available computational power for the subsequent model simulations.

2.2.5. Step 5: simulating stochastic spatial occupancy dynamics with the H-SDM

To simulate the stochastic spatial dynamics of species, extinction from and colonization of grid cells are implemented as Bernoulli random processes with probabilities according to Eq. (1) and (2) and parameterized with the 'best' parameter sets resulting from the equilibrium calibration procedure (step 4). Model simulations are performed for each parameter set separately. Each simulation starts from the observed distribution data and is run until a dynamic equilibrium is reached. The stochastic simulation is replicated to project the stochastic distribution of model outcomes. To evaluate projection reliability, model outcomes are compared to the observed distribution.

2.2.6. Step 6: analyzing alternative model scenarios

For each model scenario (step 1), interspecific dependences are applied as geographic filters (step 2), the respective model formulation is calibrated (step 3 and 4) and simulated (step 5) independently. Subsequently, projections from the alternative model scenarios can be aggregated to reflect projection uncertainty. They can also be analysed comparatively to identify how each of the alternative model scenarios contributes to projection uncertainty.

3. Case study

We aimed to analyse the distribution of Titania's Fritillary.

3.1. Available data

3.1.1. Species geographic distribution

Presence and absence data of the host plant *Bistorta officinalis* Delarbre (Adderwort) was taken from the database on Atlas Florae Europaeae (AFE - Jalas and Suominen, 1979), compiled by the AFE secretariat at the Finish Museum of Natural History (dark gray dots in Fig. 2A). Distribution data for *Boloria titania* Esper (Titania's Fritillary) was taken from a database which constituted also the basis for the 'Distribution Atlas of Butterflies in Europe' (Kudrna et al., 2011) (red crosses in Fig. 2A). In order to run the model for both species at the same spatial resolution, butterfly distribution data from about 7000 georeferenced localities were aggregated to the 50 km x 50 km CGRS grid used by AFE. For the butterfly and its host plant, the distribution data can be assumed to provide a good representation of true presences and absences, given the large spatial resolution, the aggregation of data from several decades, and a reasonably large sampling effort.

3.1.2. Environmental variables

We used monthly interpolated climate data (Fronzek et al., 2012), originally provided via the ALARM project (Settele et al., 2005) at a 10 arcmin grid resolution and aggregated it to the CGRS grid used by AFE. In accordance with Settele et al. (2008) we used aggregated climate variables: mean annual accumulated growing degree days with a base temperature of 5 °C until August, range of annual temperature (°C), range of annual precipitation (mm) and soil water content for the upper horizon (0.5 m). Soil water content was taken from the dynamic vegetation model LPJ-GUESS (Hickler et al., 2009, 2004) and represented a process-based water balance in terrestrial systems. We used averaged values for the period 1971–2000 for the climate data to match the time span used for butterfly occurrence data.

3.2. Application of the generic modelling and calibration framework

The modelling and calibration framework was implemented in statistical language R.

3.2.1. Step 1: establishing alternative model scenarios

We accounted for uncertainty in model structure and data, considering four sources of uncertainty. For each of these sources of uncertainty, we assumed two alternative hypotheses leading to a full-factorial design of 16 alternative models.

1) **Distributional data on Titania's Fritillary**

It can be expected that agricultural land-use and corresponding habitat loss constrains the range of the Alpine Titania's Fritillary population and excludes butterflies from lower (particularly Northern) Alpine regions. Therefore, the observed occurrence might not reflect the butterfly's abiotic and dispersal limited niche. To account for related uncertainties we considered two occurrence scenarios:

Occupancy observed (OO): The available distributional data

Occupancy land-use corrected (OL): Available distributional data plus grid cells at lower altitudes in the Alps that would have been climatically suitable according to the C-SDM (yellow area in Fig. 2A).

2) **Butterfly dispersal kernel**

Species specific information on the butterfly's dispersal behavior was not available. To evaluate potential impact of rare long distance dispersal (Chesson and Lee, 2005; Hastings et al., 2004), which can significantly affect projected species distributions (Holloway et al., 2016), we compared two alternative dispersal kernels:

Negative exponential kernel (exp):

$$g^{exp}(d_{ij}) = \frac{A_{cell}\exp(-\alpha d_{ij})}{\frac{2\pi}{\alpha^2}\bullet((1+\alpha d_{min})\bullet\exp(-\alpha d_{min}) - (1+\alpha d_{max})\bullet\exp(-\alpha d_{max}))} \tag{7}$$

Powerlaw kernel (pow):

$$g^{pow}(d_{ij}) = \frac{A_{cell}\, d_{ij}^{-x}}{\frac{2\pi}{(2-x)}\bullet(d_{max}^{2-x} - d_{min}^{2-x})} \tag{8}$$

where d_{ij} denoted the centre to centre distance, A_{cell} meant the cell area of 50 km x 50 km = 2500 km^2, minimum and maximum distances of cell centers $dmin$ = 33 km (was smaller than 50 km due to few smaller cells that corrected for the planar CGRS grid projection), d_{max} = 4509 km. Calibration parameters x and α were related to dispersal distance. The continuous dispersal kernels were adapted to the grid structure by an approximate normalization for total area (Chipperfield et al., 2011).

3) **Geographic extent for the equilibrium calibration procedure**

The European Alps, the Carpathian mountains, and to lower extent the Baltic states make up the main distributional range of Titania's Fritillary (red crosses in Fig. 2A). Consequently, at European scale, most grid cells are empty. Grid cells might be unoccupied because they are (i) climatically unsuitable or (ii) unreachable due to dispersal limitations. Both reasons should be distinguished during calibrations (Soberon and Nakamura, 2009). Finally, the butterfly also occurs in Russian and Belorussian areas for which occupancy maps are not available. To test the influence of the spatial extent on model calibration and projection we considered the two scenarios:

Extent all (EA): the entire area for which data was available (including an observed population in the Baltics).

Extent Central Europe (EC): a smaller area around the currently observed range in the Alps (area enclosed by blue line in Fig. 2A). EC excludes the Baltic population. In this scenario the number of observed presences and absences is roughly equal.

4) **Alternative host plant scenarios**

Distribution of the butterfly's obligate host plant *B. officinalis* strongly determines, which grid cells are accessible for the butterfly (step 2). However, the impact of ecological processes on the distribution of *B. officinalis* is largely unknown.

Therefore, prior to modelling the butterfly we modelled and projected distributions of its obligate host plant, following the same methodology (Supplementary material Appendix A). We considered two alternative host plant projections, which differed in dispersal kernels (similar to the butterfly kernels)

P1: negative exponential host plant dispersal kernel

P2: power law host plant dispersal kernel

to account for uncertainty in long-distance plant dispersal (see also Supplementary material Appendix A for further details)

3.2.2. Step 2: accounting for interspecific dependency

To account for the butterfly's obligate host plant dependence, the butterfly C-SDM (Sec. 3.2.3) and equilibrium calibration of the G-ECM (Sec. 3.2.4) were restricted to grid cells where its obligate host plant was present in the observed data (Schweiger et al., 2008). Similarly, in the H-SDM projections (Sec. 3.2.5), butterflies could only colonize and survive in grid cells where the host plant had been projected to be present by the host plant H-SDM (Supplementary Material Appendix A).

3.2.3. Step 3: modelling abiotic influence (C-SDM)

As one of the modelling approaches combining both high prediction accuracy and transferability (Heikkinen et al., 2012), we used boosted regression trees for calibrating the C-SDM. We assumed a binomial error structure and used a logit link function. Boosted regression trees were constructed with a relatively slow learning rate of 0.005, to obtain optimal model fits (Elith et al., 2008). We allowed up to three-way interactions among climate variables. To avoid overfitting, we identified the appropriate number of trees contributing to the final model by analyzing 10-fold cross-validated predictive deviance (Elith et al., 2008). We also weighted absences to ensure a prevalence of 0.5 (see Maggini et al., 2006).

3.2.4. Step 4: modelling ecological dynamics and equilibrium calibration

We calibrated parameters e (Eq. (1)), c and M (Eqs. (2)–(3)) in the G-ECM as well as either x or α depending on the dispersal kernel scenario (Eqs. (7) or (8)) using Eqs. (5) and (6) as described in Sec. 2.2.4 (using function "improvedLHS" from R- package "lhs"). For the hierarchical LHS, we first generated 400 parameter combinations for the dispersal parameters M and x or α respectively. We secondly generated 400 parameter combinations of e and c. The total sample contained 160,000 parameter sets from the full factorial combination of the two samples. Initial parameter ranges are shown in Fig. 3 . We selected the ten 'best' parameter sets that resulted in the ten lowest negative log likelihood values to exemplify the variability of the outcome due to parameter correlation.

3.2.5. Step 5: simulating stochastic spatial occupancy dynamics

We performed stochastic dynamic projections with the H-SDM according to Sec. 2.2.5 for the ten best parameter sets. Each simulation ran for 1000 time steps to ensure that the model reached equilibrium conditions. For each parameter set, we repeated the stochastic simulation 100 times. Note, because *this* study focused on testing performance of the calibration method only, we did not project the model under climate change conditions (i.e. $H_i(t)$ is constant over time in our case study).

3.2.6. Step 6: analyzing alternative model scenarios

The first three sources of uncertainties (see step 1) resulted in eight model scenarios that affected butterfly calibration, resulting in 8 × 10 suitable parameter sets. Projection models were then parameterized with each of these parameter sets and additionally the two alternative dynamic host plant projections (fourth source of uncertainty, see step 1), which resulted in 160 differently parameterized models in total. Each of these stochastic models were repeated 100 times, which summed to in total 16,000 simulation runs.

3.3. Statistical analysis

3.3.1. Model performance

We evaluated discriminative model performance (Lawson et al., 2014) by calculating the area under the receiver operating characteristic curve (AUC - R-package ROCR) for the C-SDM calibration (step 3), the equilibrium calibration procedure using the G-ECM (step 4) and the dynamic occupancy projections of the H-SDM (step 5). Since we do not translate the resulting occurrence probabilities of a particular step into presence-absence data but rather use them as direct input for the subsequent steps, we rely on AUC as a threshold-independent measure of model performance. In addition to AUC, we also considered probabilistic versions of accuracy and sensitivity (Bennett et al., 2013; Lawson et al., 2014) if appropriate and visually compared spatial model projections to observed geographic occupancy data. For the C-SDM, AUC calculations were based on 10-fold cross validation for the data restricted to host plant presence. For projection results from the G-ECM equilibrium calibration, AUC values were calculated separately for each selected parameter set. For the H-SDM, we estimated the probability of grid cell occupancy for each of the modeled calibration scenarios at the end of the simulation, after it had reached equilibrium from 100 replicates, before calculating the respective AUC values. For the G-ECM equilibrium calibration and the dynamic occupancy projections with the H-SDM, standard procedures for cross-validation are not applicable since random exclusion of grid cells would disturb the structure of spatial grid cell connectivity, and potentially impact model calibration (Moilanen, 2002).

3.3.2. Parameter sets from the equilibrium calibration procedure

We analysed correlations among model scenarios and selected parameters. Parameter correlations were linearly decomposed by PCA and associated to model scenarios (R-package vegan; see also Borcard et al., 2011). From inspection of scatter plots among parameter values (see Supplementary material Appendix B, Fig. B.1), we derived a non-linear combination that accounted for relations among model parameters:

$$z = \frac{M \bullet c}{e} \tag{9}$$

The aggregated parameter z can be interpreted as turn-over.

3.3.3. Parameter sets from the stochastic dynamic occupancy projections

From the stochastic dynamic H-SDM projections (Fig. 1, step 5), we calculated the quasi-stationary means and standard deviations of the number of occupied grid cells and compared them with the observed number of occupied grid cells. These statistics aggregated the 100 repetitions, the spatial extent of projections and the last 50 time steps of the simulation. By assuming quasi-stationarity, we reflected the current situation, where indeed the species exists and is observed (Kudrna et al., 2011). Quasi-stationarity was achieved by excluding parameter combinations from the analysis where the butterfly population went extinct during simulation runs. This procedure eliminated some extreme and ecologically unrealistic parameter combinations. Spatially resolved probabilities of grid cell occupancy were calculated as means over the projected presences and absences at the end of the simulation from all replicates of a modelling scenario.

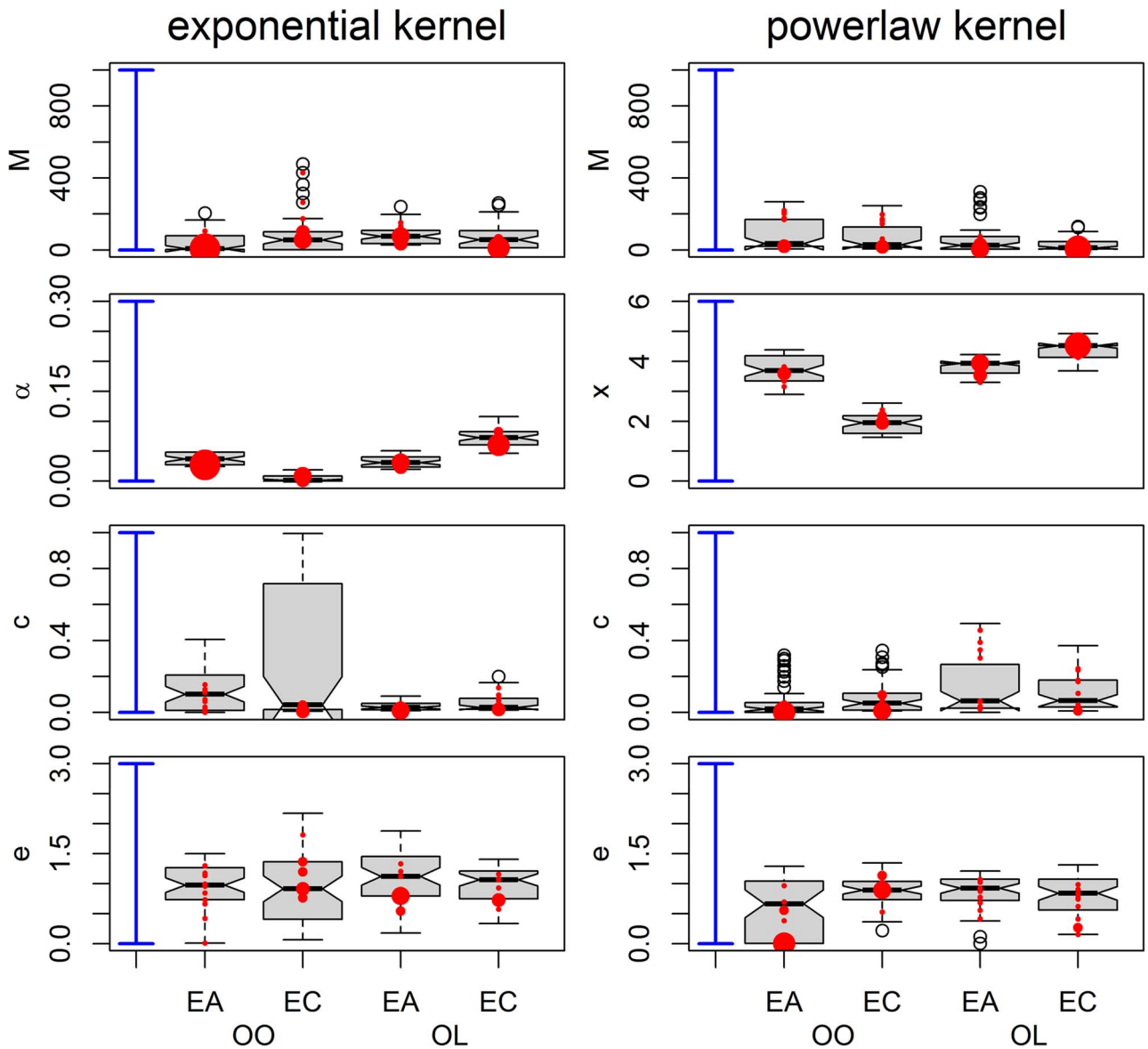

Fig. 3. Distribution of parameter values selected by the equilibrium calibration procedure assuming different model scenarios. Box-plots represent the best 50 parameter sets, while red dots indicate the 10 best parameter sets that are used for further analysis. The size of dots indicates the frequency of the selected value. (Repeated sampling of similar values is promoted by the applied hierarchical latin hyper cube). The blue bar at the left of the graph indicates the range of parameter values. Model scenarios are OO: observed occupancy, OL: land-use corrected occupancy; EA: extent all, EC: extent central Europe. Parameters M, α/x and c relate to grid cell colonization, while parameter e relates to extinction from grid cells. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Results

4.1. Calibration of the C-SDM

AUC of the C-SDM was 0.90. The C-SDM projection (step 3) covered the current range of the butterfly, however, it further indicated climatically suitable conditions in other mountainous areas and in Scandinavia (Fig. 2B), which are unoccupied. The potential Scandinavian range is currently not suitable due to the lack of the host plant (see gray dots in Fig. 2A and Schweiger et al., 2008).

4.2. Equilibrium calibration procedure

When parameterized with the selected suitable parameter sets of the equilibrium calibration procedure (step 4), the G-ECM equilibrium solution (Eq. (5)) closely reproduced the observed occupancy pattern (for an example see Fig. 2C). For each of the selected parameter sets, probabilistic accuracy (i.e. the average probability to correctly project butterfly occupancy on a grid cell where host plants occur) ranged between 0.93 and 0.94. In contrast, sensitivity (the average probability to correctly project only butterfly presence) ranged between 0.68 and 0.81. This indicated that the model better projected absences than presences. The AUC values for all 80 selected parameter sets (10 best sets for 8 butterfly-related modelling scenarios) were 0.96. High probabilities of butterfly occupancy could be expected only around the butterfly's current range (Fig. 2C).

In all model scenarios, initial ranges for the parameters were reduced (Fig. 3). Calibrated ranges for *M*, *e* and *c* were rather similar whereas calibrated ranges of dispersal distance related parameters *x* and *α* varied among the scenarios. This variation could not be attributed to one specific calibration scenario (Fig. 3).

The equilibrium calibration procedure delivered different parameter sets that performed equally well (Table 1 and Fig. 3). This is not surprising as Eqs. (4) and (5), respectively, can generate equal mean cell occupancy with different but correlated extinction and colonization parameters.

Table 1
Standard deviation (in bold on the diagonal) and correlation among calibration parameters (see Eqs. (5), (7) and (8)) resulting from the equilibrium calibration procedure.

Exponential butterfly dispersal kernel				
	M	α	e	c
M	**80**			
α	−0.41	**0.023**		
e	−0.027	−0.24	**0.28**	
c	−0.53	0.21	0.26	**0.040**

Powerlaw butterfly dispersal kernel				
	M	x	e	c
M	**51**			
x	−0.50	**0.98**		
e	0.11	−0.40	**0.26**	
c	−0.47	0.32	0.38	**0.12**

Variation of suitable parameter values could be explained as follows. Firstly, we identified a dynamic and a static solution in the equally well performing parameter sets (Fig. 3, Supplementary material Appendix B, Fig. B1). The dynamic solution was characterized by turnover in grid cell occupancy (i.e. non-zero values of *e* and *c*). In the static solution, turn-over was suppressed (i.e. nearly zero values of *e* and *c*). As the static solution only reproduces the C-SDM, these parameter sets were excluded from further analysis.

Secondly, a principal component analysis (Fig. 4) that reduced dimensionality of the parameter space revealed the correlation among the parameters (Table 1). The first two axes explained more than 80% of variance. The first axis was related to colonization parameters *M, c* and *α* or *x*, the second axis to the extinction parameter *e*. The aggregated variable *z* (Eq. (8)) subsumed the correlations. Using the aggregated parameter *z* in the PCA, parameter sets arranged along the *z*-direction, but clustered (parallel shift) according to specific α values (Fig. 4C, D).

4.3. Stochastic dynamic occupancy projections

Stochastic dynamic occupancy projections of the H-SDM (step 5) using the best parameter sets of the equilibrium calibration procedure (i.e., the 10 best sets of step 4 for each of the 16 model scenarios) performed worse than projections of the equilibrium calibration procedure. Mean of all AUC values calculated for each of the 160 projected parameter sets was 0.81 (standard deviation 0.15) and increased to 0.84 (± 0.12), if we used only the single best parameter set of each projection scenario.

Interestingly, in the dynamic stochastic occupancy projections, the butterfly exceeded the observed range and occupied regions further north to the Alps (Fig. 2D). Moreover, the dynamic projections suggested only a very low occupancy in the Baltics and Southern Finland in contrast to the observations (compare crosses in the Baltics and Southern Finland (North-East) in Fig. 2A and that are not reflected in Fig. 2D)

The projected numbers of occupied grid cells varied among sets of selected parameters, and scattered around the observed occupancy (Fig. 5). The aggregated parameter *z* was a good predictor for projected occupancy (Fig. 5I, J). Butterfly occupancy to a minor degree also depended on the underlying host plant projection, where we found that projection P1 caused butterfly occupancy to be slightly lower than projection P2.

Most importantly, for some parameter combinations (*z*, *α* or *x* and host plant projection), the model closely projected the observed butterfly occupancy (see Fig. 5).

5. Discussion

We suggest a generic framework to calibrate hybrid species distribution models (H-SDMs) from maps of species occupancy and variables describing environmental conditions (Sec. 2.2). In contrast to other H-SDMs (reviewed in Fordham et al., 2013), our framework requires only weak (or incomplete) independent information on biotic processes and factors.

Tackling the problem of lacking mechanistic biotic information about the species spatial population dynamics, model construction was confronted with three major challenges concerning (i) spatial and (ii) temporal scales as well as (iii) process detail (which can encompass several independent processes). Our suggested solutions enable the construction of model-based projections of species distribution dynamics, even if critical dynamic information is lacking. The lack of knowledge compromises the resolution of biotic processes in the model, and therefore the reliability of the model projections. However, due to the included model scenario analysis (steps 1 and 6) and the detailed dynamic analysis of different parameter sets (step 5) the framework is able to identify parameter sets that are in accordance with the available data and to estimate their impact on model projections. Thus, it provides crucial insight in the impact of biotic factors on the spatial dynamics of species and can reveal critical sources of uncertainty. In the following we discuss the merits and limitations of the framework on the example of the case study.

5.1. Performance of the modelling framework

The suitability model (C-SDM, step 3) reproduced the current distribution of the butterfly in the European Alps, the Carpathian Mountains and in the Baltics (Fig. 2B) and corroborated results from Schweiger et al. (2008) that environmentally suitable habitat also exists far beyond the presently observed distribution, which however is inaccessible due to host plant absence (Fig. 2A). Projections of the equilibrium solution (step 4) performed better because they revealed dispersal limitation, which restricted butterfly projections to areas close to the observed butterfly range (Fig. 2C). The stochastic dynamic projections of the H-SDM (step 5) indicated a potential for colonization of mountainous regions adjacent to the Alps, where the butterfly currently is not present (Fig. 2D). However, they also showed absence of the butterfly in the Baltic area where it is presently observed. We hypothesize that these discrepancies to the observed occupancy pattern could be caused by parameter uncertainty (e.g. from unresolved correlations), by the impact of land-use excluding the butterfly from potentially suitable areas, by a secondary host plant or that the Baltic *Boloria titania* population might be a sink in the species colonization-extinction dynamics. These points are discussed in the following.

5.2. Parameter uncertainty and correlation

There are two sources of parameter uncertainty in the calibration: (i) alternative states and (ii) equifinality, as explained below. They might also be the reason, why we could not identify a strong impact of calibration scenarios on the parameter values (Fig. 4).

We identified two alternative solutions (see Sec. 4.2): a static solution without colonization-extinction dynamics (corresponding rates are nearly zero) and a dynamic solution with colonization-extinction dynamics (and corresponding nonzero rates).

The static solution represented the C-SDM by suppressing dynamics. The existence of the dynamic solution indicates that the abiotic niche described by the C-SDM could not explain the entire distribution of the butterfly and thus points to the importance of biotic processes for this distribution.

The dynamic solution could not be uniquely resolved by model calibration. Instead we found alternative parameter sets (Fig. 3) that equally well explained the observed butterfly occupancy pattern

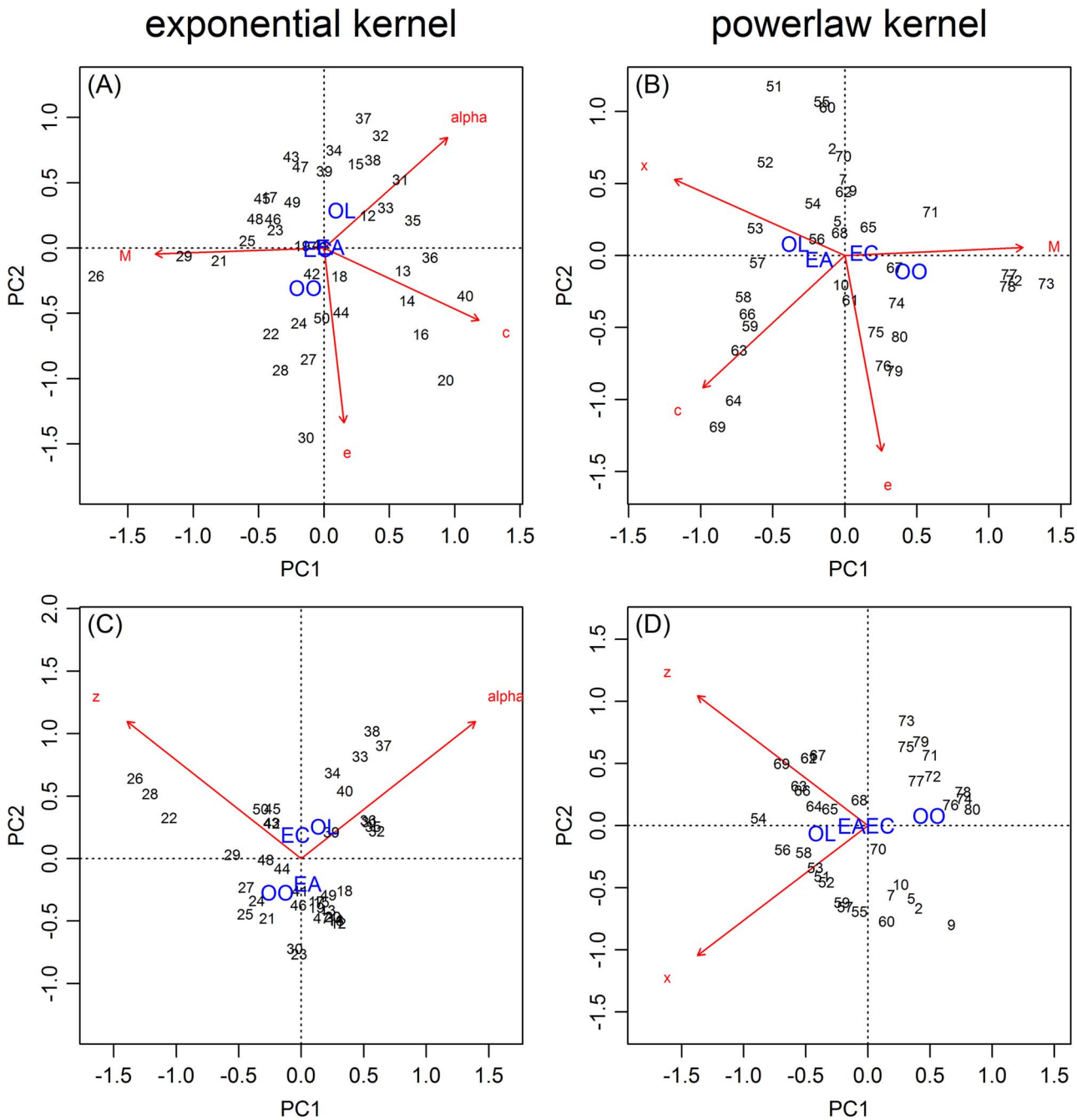

Fig. 4. Correlation biplot for butterfly (*Boloria titania*). Exponential (left column) and powerlaw dispersal (right column) kernels. The upper row displays ordination of the model parameters, while in the bottom row the aggregated parameter z is introduced. When using model parameters, the number of migrants spans the first axis, while extinction risk spans the second axis. The other two dispersal parameters seem to contribute to both axes. However, adding directional contributions of colonization related parameters indicates their strongly correlated impact on variance explained along the first axis. Introducing the aggregated parameter z sorts the parameter sets clearer along the two vectors. Explained variance (A- exponential dispersal) axis1: 49%, axis2: 32%; (B – powerlaw dispersal) axis1: 47%, axis2: 35%, (C- exponential dispersal) axis1: 62%, axis2: 38%; (D – powerlaw dispersal) axis1: 63%, axis2: 37% Model scenarios (blue colour; OO: observed occupancy, OL: land-use corrected occupancy; EA: extent all, EC: extent central Europe) only weakly correlate with selected parameter sets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(equifinality). Equifinality (Beven and Freer, 2001) indicates over-parameterization (Dormann et al., 2012) and is the result of insufficient information content in the data to parameterize the biotic processes. In this study, one possible reason for a reduction in information content could have been the sequential model calibration. If the calibrated C-SDM had incorrectly attributed biotic information to environmental factors (e.g. due to covariation), we had to assume reduced explanatory power of the latter calibrated dynamic H-SDM. Therefore, we particularly aimed at avoiding over-fitting while constructing the C-SDM (Sec. 3.2.3). We assume that the C-SDM calibration had not strongly reduced information content for the latter H-SDM equilibrium calibration.

Instead, we consider correlation among the dynamic parameters as the main calibration problem. The derived parameter z (Eq. (9)) reflects this correlation as it can be interpreted as a descriptor of grid cell turnover (i.e. the ratio between rates of local colonization of empty grid cells and extinction from occupied grid cells). In the equilibrium calibration procedure (step 4), this ratio cannot be resolved further, because equal numbers of grid cells had to be colonized and vacated in order to keep occupancy constant. Single snapshot occupancy data provide too limited information to resolve correlated biotic processes

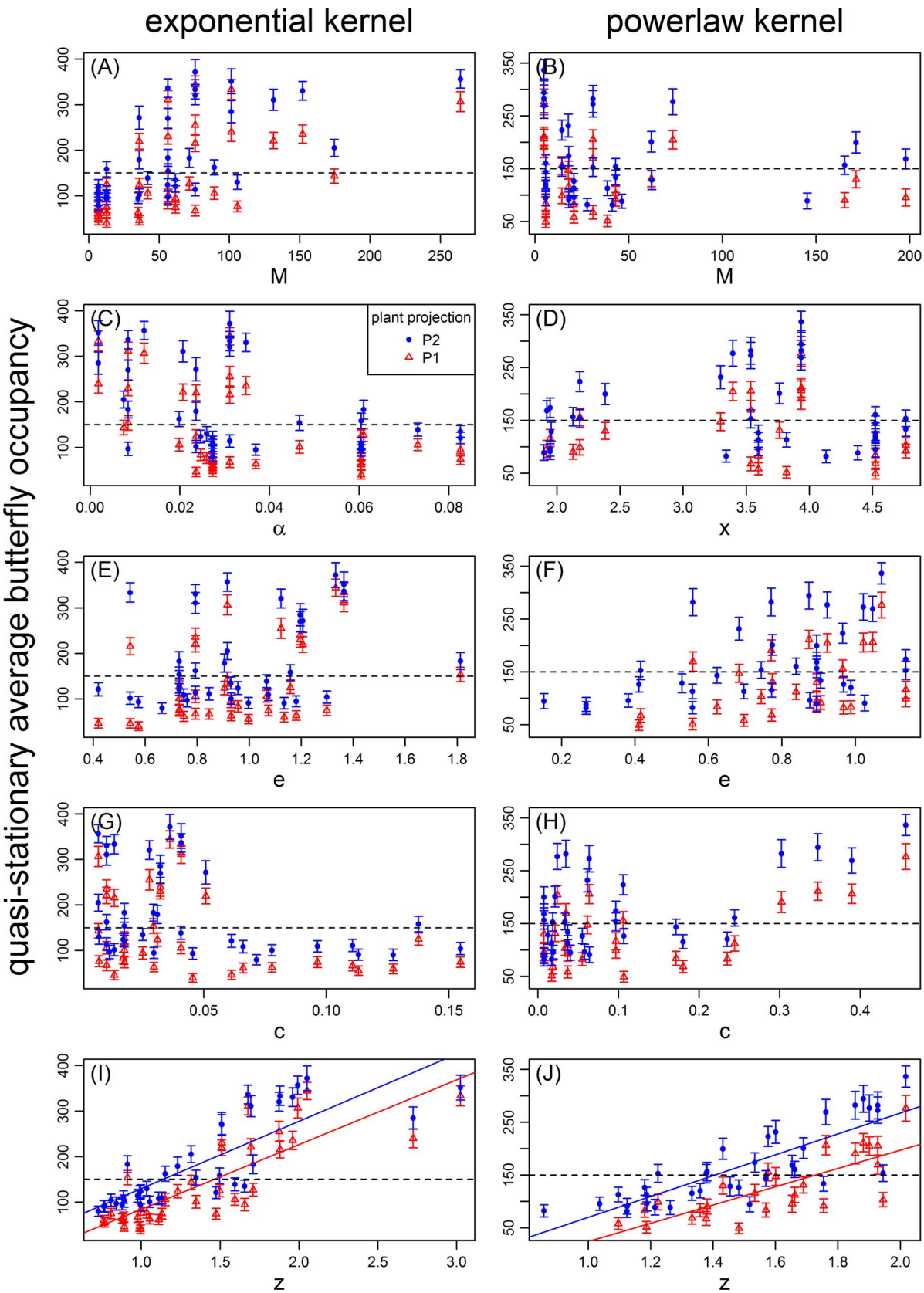

Fig. 5. Projected butterfly (*Boloria titania*) occupancy vs model parameter values (graphs A–H), trends can hardly be identified. Instead graphs I and J show that butterfly occupancy correlates better with the non-linearly aggregating parameter z (Eq. (8)). Colours indicate the underlying plant projection (red: P1, blue, P2 – see legend). The black dashed line indicates observed occupancy. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Gu and Swihart, 2003). Therefore, the subsequent stochastic dynamic occupancy projections (step 5) are essential to gauge consequences of alternative suitable parameterization for model projections.

5.3. Dispersal ability

The stochastic dynamic occupancy projections produced variations in the average grid cell occupancy (Fig. 5) even if the turn-over parameter z was constant. This variance arose from insufficient knowledge about dispersal in combination with two simplifications of the equilibrium calibration procedure compared to the full dynamics of the H-SDM. The equilibrium calibration, firstly calibrated colonization probability of empty grid cells from the species dispersal ability during a single time step (Eq. (5)). Dispersal in several steps was ignored. Secondly, being based on the first moment approximation (Eq. (4)), the equilibrium calibration procedure could not account for variability from immigration-extinction stochasticity (Hanski, 1994). In contrast, the dynamic projections allowed for subsequent random colonization events that were not immediately compensated by extinctions. Thus, variance in projected occurrence that could not be resolved by parameter z can be attributed to uncertainty about dispersal abilities of the butterfly including its stochasticity. Our analysis therefore identifies dispersal as a critical source of uncertainty in our case study.

5.4. Projected range expansion around the European Alps: does land use limit the butterfly range?

The stochastic dynamic occupancy projections of the H-SDM led to an extended range beyond the currently observed butterfly range in the European Alps (compare Fig. 2A–D). This challenges our assumption that currently the butterfly population is in equilibrium. However, given the long-term and intensive monitoring effort, we trust the observed absences of *Boloria titania* and believe that the population indeed is in equilibrium.

More likely, land use might have limited the observed species range but was not explicitly considered in the model. We found that taking into account land use impact in the equilibrium calibration procedure affected the dispersal related parameters (α and x; Fig. 3). The slightly expanded geographic range in mountainous regions, predicted by the dynamic projections (Fig. 2D) compared to the equilibrium calibration procedure (Fig. 2C), likely indicates the butterfly's potential geographic range without impact of anthropogenic land use. Thus, our analysis identifies land use as a potentially important factor for the distribution of *Boloria titania*, which agrees with findings for high latitude butterflies (Eskildsen et al., 2013).

5.5. The Baltic Boloria titania is potentially a sink population

The stochastic dynamic occupancy projections provided new important insight in the existence of the Baltic butterfly population. We found that the butterfly population in the Baltic States and Finland was projected very likely to go extinct. This result conflicts with the observed presence of Titania's Fritillary in the Baltic States and Southern Finland. There are two likely explanations for this discrepancy. Firstly, the Baltic and Finnish butterfly populations are potentially oligophagous and might utilize *Viola* species as a secondary host plant (see supplementary information in Pöyry et al., 2008 for the observed feeding behaviour in Finland and Northern Europe). Since we do not have reliable distribution data for *Viola* species nor detailed information about the possible density-dependent benefits of a secondary host plant, we could not consider such effects in the model. A secondary host plant might enhance the suitable butterfly area. Secondly, the Baltic and Finnish populations might be connected to larger populations in Russia (Kudrna et al., 2011). For these populations, reliable occupancy data is not available, which restricts the spatial extent of our study. However, the impact of the spatial extent on parameter estimates (including or not the Baltic and Finnish populations and the Eastern border - see Fig. 3) was low because only grid cells at the Eastern border of the modeled area should be affected (Moilanen, 2002). Given the fact that ignoring the Eastern butterfly range in our dynamic occupancy projections, the Baltic and Finnish populations likely went extinct in the model, we hypothesize that these populations could be sink populations, connected to a source east of the modeled area (Moilanen, 2002 on biased occupancy projections due to disconnection of patches). Source-sink dynamics have been considered one potential source of bias to static species distribution models but can be revealed with demographic approaches (Pagel and Schurr, 2012).

6. Conclusions

We present a hybrid modelling and calibration framework to project species distributions, taking into account demographic processes and dispersal. The framework is distinct in its attempt to be calibrated from widely available data on geographic distributions of species and environmental factors. Relying on rather low data requirements, the framework can potentially be applied to a wide range of species. However, the small information base also reveals knowledge gaps that impact model projection reliability.

A problematic knowledge gap is the lack of data to inform spatial population dynamics (e.g. time series of species distributions or species specific functional trait information). Particularly, the available information is not sufficient to resolve correlation among colonization and extinction processes. This causes uncertainty in the species dispersal ability and subsequently in the range projections, even assuming temporally constant environmental conditions. Under environmental change, we expect uncertainties to even increase.

To cope with the lack of knowledge, we suggest within the framework extensive and detailed analyses of the data and structural gaps (step 1) and of the results of the modelling and calibration steps 2–5 (Fig. 1). In particular, step 5 (the stochastic dynamic projections of the H-SDM) is essential as it selects the dynamic biotic processes (species extinction and colonization rates including dispersal distances) that most likely reflect the data. The model scenario analysis (step 6) is important as it allows evaluating projection reliability. Model scenarios that provide biased projections of current occupancy should not be ignored, but thoroughly investigated as they provide insights in confounding factors and achievable projection reliability.

Executing the steps of the framework narrows the parameter range and reveals critical knowledge gaps that can compromise projection reliability (e.g. the lack of data to inform the population dynamics or dispersal processes). Further, it can explain mechanisms that drive the propagation of uncertainties. With the presently available data, the framework cannot be expected to provide highly reliable quantitative projections of species distributions. Instead, it can enhance mechanistic understanding of the species range dynamics, estimate the reliability of species range projections, and reveal, which additional data would improve projections. This is often the best possible achievement to support management facing data limitations (Singer et al., 2011). Very importantly, this framework provides potential agendas for field related research to improve and tailor the collection of biotic parameters.

Declaration of interest

None.

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Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.02.002.

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